QUANTITATIVE EVALUATION OF THE ASSOCIATION BETWEEN VEGETATION AND SOIL IN THE TUNDRAL ZONE

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Questions of the interaction between components of ecosystems or biogeocenoses is now receiving concentrated attention from representatives of many special fields. Two approaches in this direction are possible: investigation of the processes of rotation of materials and energy in the ecosystems and establishment of the dependence between component changes both in space and time. These two approaches are equally important for an understanding of the regularities of structure and function of ecosystems and biogeocenoses,* but the second is, for the present, much less popular.

Considering that all connections in biogeocenoses have a probability (stochastic) nature, the relationships between the components must be demonstrated on mass material by using the methods of mathematical statistics for its treatment. Only by this means can the actual existing associations be determined and the chance variation connected with the effect of unstudied factors be eliminated. Comparison of a single pair of observations and the establishment of a single difference does not usually justify any basic conclusions. Such differences may be purely chance, and V. N. Beklemishev (1931) was perfectly correct when he wrote that nothing has brought so much harm to biology as the method of a single difference.

The purpose of the present work is to establish the quantitative dependence between vegetation and soils. This is quite an extensive problem and, depending on the raising of concrete questions, it may be solved by various methods. It is possible to show the association of abundance or occurrence of individual plant species and individual features of the soils (moisture, humus content, potassium, phosphorus, pH, etc.) with the assistance of coefficients of correlation and correlational ratios. These methods are often used by geobotanists. But we wished to explain how the plant association as a whole, i.e., the entire company of its species, reacts to changes in the soil, also examining the soil as a whole and not its isolated features. Having described the vegetation and the soil by means of two groups of variables (indices), we could have established the dependence between these objects by the method of canonic correlation (Anderson, 1963). But this method requires a detailed quantitative study on a large number of sites and vegetation as well as soils. Such an investigation of soils is extremely difficult and, therefore, we took another course: a comparison of quantitative data on vegetation with qualitative data on soils.

The approach which we develop here is similar in aims and principles to the method of complex ordination of V. B. Sochava et al. (1967), although in our opinion it is not ordination but a method of determination of the leading factors of the environment. The work was accomplished on materials collected in the summer of 1967 at the Taimir Station of the Botanical Institute of the Academy of Sciences of the USSR in the neighborhood of the suburb Tarei located on the midcourse of the river Pyasina. Four types of tundra were selected and one type of polygonal swamp.

1. Small-hummocky sedge–dryad green mossy tundra occupying large areas on quite flat portions of watersheds and on sloping declines. Characteristic for these tundras are small-hummocky nanorelief and a mosaic character of the moss layer formed mainly of Tomenthypnum nitens, Aulacomnium turgidum, Hylocomium splendens var. alaskanum, and Dicranum congestum. In the herbaceous layer the greatest role

* By ecosystem we understand an aggregate of living organisms along with the environment, interacting together; and by biogeocenosis, the spatial individuality characterizing the homogeneity of all its constituent components (Vasilevich, Ipatov, 1969).

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ed by Carex ensifolia and Dryas punctata. The soils in these tundras form a nanocomplex of four types of soil alternating with small areas with an extent of 20-100 cm (for more details on the vege- and soils of this type of tundra, see the article of Boch, Vasilevich, and Ignatenko, 1969).

2. A spotty sedge–dryad green mossy tundra is also widely distributed in the region of this It is located on the highest portions of the ridges and crests as well as on the upper parts of pes. The dominating species are approximately the same as in the preceding type. The vegetation e tundras may be considered as a three-membered complex consisting of fragments of associations spots, in varying degree of overgrowth, the liverwort mosses, crustose lichens, and blue-green redominate. On the edges of the spots are low cylinders, "borders," and in the fissures around them nosses predominate. The complexity of the vegetation cover is accompanied by a complexity of soils.

. Legume–dryad fissure-spotty tundras are regularly encountered on the highest ridges, on ltops, etc. Usually they are connected with a lighter mechanical composition of soil. The mosses is quite small here as compared with other tundral types. In the herbaceous-shrub egumes (Astragalus subpolaris, A. umbellatus, Oxytropis adamsiana) and dryads play a large he area of the association is broken with narrow fissures averaging individually 50 × 50 cm.

. Salix–dwarf birch green mossy swampy tundras are adapted to the lower portions of the water- mainly to the summits of the disintegrated areas and the edges of the swamps. The species com- here is poorer than in other tundral types. The principal plant species are Retula nana, Salix , S. pulchra, and E. angustifolium. In the moss layer, in general the same complex of dom- tundral species is retained, but the abundance of T. nitens diminishes and a quite substantial re of Sphagnum subsecundum, Drepanocladus uncinatus, etc., appears.

Flat polygonal swamps occupy large areas in every kind of depression in the mesorelief on the ed. Each flat polygon, from 10 × 10 to 20 × 20 m in size, is separated from the neighboring poly- quite wide (up to 1 m), very wet, fissure-channels. Distributed on the flat polygons are complex associations with a predominance of Salix reptans, S. pulchra, Dryas punctata, and Carex stans. In s cover the same species predominate as in the tundras. In the fissure-channels a quite homoge- egetation predominates, consisting mainly of C. stans and mosses of the genera Drepanocladus, on, and Campylium.

each of these tundral and swamp types, two transects were made, each 10 m long. The vegetation transects was described according to abutting sites measuring 20 × 25 cm. The short side of the located along the transect. Thus, each transect consisted of 50 sites on which each species cover d.

the entire length of the transect, soil trenches were dug, along which the morphology of the soil as investigated. In characteristic places samples were taken for chemical analysis. Every 10 the course of the transects, measurements of the nanorelief and of the permafrost level were hen on each transect soil types were isolated and the descriptions of vegetation on the sites were d into corresponding groups. Sites falling on the boundaries between soil types were not included r treatment.

establish the connection of vegetation with soil types, it was necessary to determine whether the n differs on the isolated soil types and how strongly. As a set of indices to assist in characteriza- e plant composition on the site, we selected the species cover. The degree of differences between determined as the distance between them in a multimeric system of coordinates (in multimeric ere the cover of individual species serves as axis. This value is calculated by the formula

$$R_{ij}^2 = \sum_{k=1}^{m} (x_{ik} - x_{jk})^2,$$

and x_{jk} are the covers of k species on comparable sites i and j. In order to diminish the role ting species in a determination of degree of differences between sites and to enhance the role of ith small cover, before beginning the treatment the square roots were extracted from all values vers. Such a transformation of data has been used by us previously and has been fully justified h, 1967).

n group of sites corresponding to a definite soil type within the limits of the transect may be char- by the average representing the abstract site (it may be called the typical). On this site the values

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for the species covers are the arithmetical average of the cover values and, more precisely, of their square roots, for sites of a given group. The differences between groups of sites, and consequently also the difference in vegetation on different soil types, are determined by the distance between average sites (centers of the groups) in the same multimeric space. These differences may be compared with the variation of vegetation within the limits of one soil type. This value we determine as the average square of the distance in a multimeric space of sites of a given group from its center, which is analogous to dispersio

With these two characteristics, criterion t may be used for comparison of the vegetation of these s groups

$$t = \frac{(M_1 - M_2)}{\sqrt{\frac{\bar{R}_1^2}{n_1} + \frac{\bar{R}_2^2}{n_2}}},$$

where $(M_1 - M_2)$ is the distance between the centers of the groups, R_1^{-2} and R_2^{-2} are mean squares of the distances of the group members from their centers, and n_1 and n_2 represent the number of sites in the group. If t exceeds the limiting value at a 95% level of significance, then the difference between site gro may be considered reliable. And this shows that the vegetation, or more accurately the species composition and relationship of species as to cover, differs substantially on comparable soil types. In other words, it may be stated that the vegetation reacts to existing differences in the soils.

Such treatment was carried out within the limits of each transect. It appeared that by no means eve soil type bears specific vegetation. Thus, for example, in transect 6 in small-hummocky sedge–dryad gr mossy tundra, four soil types were found: tundral humus–gley, tundral gley sod, swampy-tundral humus gley, and swampy-tundral peat–humus–gley. In vegetation, only the tundral gley sod soil differed from the others. This case is examined in more detail in our previous work (Bloch, Vasilevich, and Ignatenko 1969).

With the assitance of criterion t, the substantiality of differences may be established, but it is mu more convenient to express the quantitative role of differences between soil types in the determination o differences in vegetation by means of dispersion analysis.

In conducting a dispersion analysis, the complete variation of the vegetation in the transect was broken down into two components: 1) variation within soil types and 2) variation between soil types. In order to calculate the sum of squares of deviation for variation of the vegetation within soil types, all squares of distances of individual sites from the centers of their groups must be combined. By dividing this sum by the number of degrees of freedom, we obtain an evaluation of the intragroup dispersion.

The intergroup dispersion is obtained as follows: the squares of the distances between all pairs of average sites (group centers) are calculated. Their sum is divided by the number of comparable pairs, i.e., by C_n^2, where n is the number of groups. By this means we obtain the average square of distances between group centers, and the dispersion of the group centers is half this value, which has been shown previously (Vasilevich, 1967).

Comparison of these two dispersions is done with criterion F. But, first, the intergroup dispersio should be multiplied by the number of groups. When the volume of the groups differs, then, according to the recommendations of Snedeker (1961), the intergroup dispersion is multiplied by the value

$$n_0 = \frac{1}{a-1}\left(\sum n_i - \frac{\sum n_i^2}{\sum n_i}\right),$$

where a is the number of groups and n_i the number of i-groups.

In Table 1 are presented the results of the dispersion analysis of individual transects. Here we gi only the sums of the squares of deviation within the groups, between groups, and the percent of the total squares, arriving at the variation between soil types. The latter value shows to what degree variation of the vegetation is determined by differences between soil types. The higher this value, the closer the connection between vegetation and soils. In all transects except the eighth, the relationship of intergrou to intragroup dispersion exceeds the limit at a 95% creditable level. Consequently, in these transects th vegetation reacts to differences in soils and at least some soil types carry a specific vegetation.

TABLE 1. Dispersion Analysis of the Connection between Vegetation and Soils within the Limits of Individual Transects

Type of tundra and swamp	Transect No.	Components of variation			% variation determinable by soil types
		within soil types	between soil types	total	
Flat polygonal swamp.	3	890	1290	2180	59
	10	1364	870	2234	39
Swampy tundra	1	1518	434	1952	22
	4	1675	862	2537	34
Spotty tundra	5	1026	379	1405	27
	7	975	365	1340	27
Small-hummocky tundra	6	1048	457	1505	30
	2	1304	180	1484	12
Fissure-spotted tundra	8	1011	194	1205	16

ccording to how close the connection of vegetation with soils, the types of tundra and swamp under ay be divided, although provisionally, into three groups.

ansects 3 and 10 form the first group, located on the flat-polygonal swamp. They have the highest of vegetative variation connected with soil differences (59 and 39%). Such strong differences are d by the fact that in this case the plant groupings and the soils are adapted to different elements icrorelief and not the nanorelief as in all tundral types that we have investigated. Two soil types ered in this type of swamp differ quite strongly: swampy-tundral peat–gley in the central part of gon and swampy-frozen peat–gley soil in the fissure-channels.

e swampy-frozen soil under the fissure-channels has twice the thickness of the peat and also a acid, but not strongly acid, reaction; less ash; a reduced content of exchange bases; somewhat stores of mobile phosphorus; and an enrichment of the upper part of the peat layer with mobile potas- he swampy-frozen soil is formed in meadow marshes under conditions of constant excess moisture and d inundation. Moreover, under these conditions each component of the soil microcomplex is of extent, which permits groupings of vegetation of a more definite composition and complexity to hem.

e second group is made up of the marsh-ridden, spotty, and small-hummocky tundras. Here the on of vegetation with soils is less intimate. Soil differences determine only 15-30% of the varia- e vegetation.

e soil cover of the spotty tundras is characterized by a four- or five-membered complex of tundral gley soils on the main surfaces, tundral gley sod soils in cylinders, tundral residual-gley the spots, and swampy-tundral peat– and peat–humus–gley soils in depression-channels. ochemical characteristics the soils of a given microcomplex differ markedly from each the soil of the main surface the upper mineral layers are sandy, but in soils of the borders and y are medium sandy. The highest hydrolytic acidity (11.9 meq) is in the soil of the main surface, west is in soil of the spots (1.5-2.1 meq). The content of humus and nitrogen is reduced in the ection. The intensive dynamic processes occurring in the soils of spotty tundras no doubt reduce ction of soils and vegetation. The overgrowth on the spots usually outstrips the soil development.

sh-ridden tundras are characterized by an alternation of smooth surfaces and small hillocks and ns. On the smooth surface, swampy-tundral humus–gley and swampy-tundral peat–humus–gley soils n chemical composition these soils are very similar. The latter differs only in a slightly more acid re- ayer A_T and A_0A_1, in a raised content of exchange bases, and in a higher hydrolytic acidity. In small de- , swampy-tundral peat–gley soils develop, differing from the former by the absence of a humus layer dium decomposability of the peat. Under weakly expressed hummocks are tundral gley and tundral soils. They differ from swampy-tundral soils by the absence or slight thickness of organogenic l by somewhat less gley, a more acid reaction, less humus formation, and lower stores of mobile otassium.

e small-hummocky tundra we also find alternation of two to four soil types. The areas occupied l type extent 20 to 100-150 cm. Swampy-tundral humus–gley and swampy-tundral peat–humus s are very similar. The latter differs by the presence of a peat layer with low ash content, in drolytic acidity, and in a high content of exchange bases. In chemical composition they have a

TABLE 2. Dispersion Analysis of the Connection of Individual Plant Groups with Soils

Transect No.	Plant group	Sources of variation	Total of squares of deviation	Number of degrees of freedom	Average square of deviation	% variation determinable by soil types	P (F)
2	Mosses	Between groups. . .	68	1	68,0		
		Within groups. . . .	773	41	18,8	7,5	>0,05
	Lichens	Between groups. . .	28	1	28,0		
		Within groups. . . .	131	41	3,2	17,5	<0,01
	Flowering	Between groups. . .	29	1	29,0		
		Within groups. . . .	398	41	9,7	6,8	>0,05
6	Mosses	Between groups. . .	321	3	107,0		
		Within groups. . . .	631	39	16,2	34	<0,01
	Lichens	Between groups. . .	52	3	17,3		
		Within groups. . . .	149	39	3,8	26	<0,01
	Flowering	Between groups. . .	88	3	29,3		
		Within groups. . . .	276	39	7,1	24	>0,01

number of features in common with the tundral humus–gley soils. In all three soils there is a surface organogenic layer with considerable stores of humus, potassium, and exchange bases. The listed nutritional elements enter principally into organic residues, however, and are poorly accessible to plants.

A special place in the nanocomplex is occupied by tundral gley–humus soils adapted to nanoincreases and characterized by increased drainage and the most favorable water–heat characteristics. In transect 2 there are no such soils; thus, the soil cover appears more equalized, which also affects the vegetation. Here only 12% of the vegetative variation is connected with soil differences.

The third group is the fissure-spotty, legume–dryad tundras. Here tundral sod soils develop. We divide them into thick, thin, degraded, and residual. In chemical composition these soils are very similar and differ only in humus content. In the soil of the humus polygon (level A) is contained 3.15-3.95%, in the soil of the bare polygon 1.7-2.9%, and in the soil of the fissure 4.3-4.4% humus. Soils of the fissures also have a somewhat high acidity. These differences did not affect the vegetation. Its variation within the limits of these soil types completely masks the differences between them.

The method used permitted not only an evaluation of the role of soil differences in the variation of vegetation but also a determination of the minimal differences in soils to which vegetation reacts.

So far as we know, no one has given such a quantitative evaluation of the role of soils in the variation of vegetation; therefore, there was nothing with which to compare the results. We attempt to establish, as it were, in first approximation what may be the top and bottom of the limits for percentage variation in the vegetation determinable by soil differences. As for the upper limit, it is clear: the sum of squares for variation between soil types never consists of 100% of the total variation. Also, with completely homogeneous soil conditions the vegetation will vary, since there is always a more or less clearly expressed mosaic character of the plant society determinable by the character of vegetative multiplication of species. Moreover, there is always the action of chance factors not connected directly with natural circumstances in a given plant society, and also a floristic and cenotic defect in the whole plant societies and in their parts. Considering all these facts, it would follow that, for determination of the upper limit, the sum of squares of deviation in absolutely homogeneous conditions of the environment should be calculated and removed from the total, but so far we do not have methods for solving this problem.

Apparently it may be considered that the maximal possible percent of vegetative variation due to differences in soil type will not exceed 70-80%. The lower limit is determined by those differences in vegetation which still appear authentic. With the site size and selection volume in our work, this limit is approximately 10-15%.

On the basis of the given limits, the connection of vegetation with soil types in flat-polygonal swamp may be considered quite intimate, and in spotty and swamp-ridden tundras, medium. In small-hummocky tundra this dependence is medium or weak, and in fissure-spotty tundra a slight connection of vegetation with soils appeared untrustworthy.

TABLE 3. Dispersion Analysis of Vegetative Variation within the Limits of Soil Types

Soil type	Transect No.	Sources of variation			% vegetative variation determinable by transect differences
		within transect	between transect	total	
Tundral residual-gley	5; 7	846	91	937	9,8*
Tundral gley sod	5; 7	395	122	517	23,6*
Tundral gley	1; 4	223	217	440	49,4
Swampy-frozen peat–gley	3; 10	645	498	1143	43,5
Tundral humus–gley	5; 6	828	197	1025	19,2
Tundral gley–peat	2; 4	758	400	1158	34,5
Swampy-tundral humus–gley	4; 6	643	485	1128	43,0
Swampy-tundral peat–humus–gley	1; 2; 4, 6; 7	1161	1110	2771	40,1
in swamp-ridden tundra	1; 4	524	298	822	36,3
in small-hummocky tundra	2; 6	1055	139	1294	10,7*
Swampy-tundral peat–gley	1; 3; 4; 10	3440	1806	5246	34,5
in swamp-ridden tundra	1; 4	1850	344	2194	15,7
on swamp	3; 10	1590	965	2555	37,7

* Differences not significant on 95% reliability level.

ry method of study has definite limitations and inadequacies. Our method, of course, is no ex- the general rule. We did not take into account the variation of soil indices within the limits of soil units. It is quite possible that some part of the vegetative variation is connected with soil within their types. But if differences in soil types often determine only 20-30% of the vegetative then this source of variation will hardly account for very much, apparently no more than 3-5% iority of cases.

width of the sites used is 25 cm, and, although we discarded those falling on the borders be- types, there is no guarantee that all borders show a perpendicular transect. It is possible of the sites which we kept and included in the transect intersected soil boundaries. This of finitely distorted the results, but we did not see how to avoid it. The method of linear transects ically more irreproachable in this respect, but it requires transects of a much greater extent, site for the linear transects is very small and in each individual portion the vegetation is taken deration very imprecisely.

ie majority of cases the elements of the soil nano- and microcomplexes were of small extent. probable that in such a situation the penetration of plant roots from one soil to another is indi- ch makes a connection of vegetation with soils less intimate. To check this, in both transects ll-hummocky tundra, calculations were done independently for mosses, lichens, and flowering ble 2). The results of this treatment show that for flowering plants the percent variation de- by differences in soil types does not differ notably from this index for mosses and lichens. It that the roots of flowering plants penetrate neighboring soil types; therefore, it may be con- at this feature does not play a serious role in determination of the degree of differences in vege- arious elements of the soil nanocomplex.

nade an additional comparison of vegetation on the same soil types but in different transects :h in a single and in different types of tundras. The results are presented in Table 3. Of 15 soil y nine are presented here, since the remaining six are encountered in only one transect. The are found in only one type of tundra and swamp and the other two in two transects within the limits of This makes possible an evaluation of the vegetative differences on one soil and in one type of swamp, which are significant in three of eight cases. Moreover, the percent variation relating ces between trenches is no lower here than between trenches in different types of tundra and he differences between transects determine 10-50% of the vegetative variation within the limits types. The allotment for chance variation is apparently small, since sufficient averaging of hin the limits of the trenches is carried out.

rently one of the most important factors determining vegetative differences on the same soil rent transects is a cenotic defect and ecological replaceability of the species types. In one erhaps one species is abundant, in another, another species which is, however, close to the first

ecologically. For example, in transect 3 of flat-polygonal swamp Calliergon richardsonii and C. stramineum are very abundant in the fissure-channel, but in transect 10, Campylium polygamum and Drepanocladus uncinatus. As a whole, the differences in the vegetation within the limits of one soil type in different tundras are determined primarily by the connection of the vegetation with other factors of the environment not associated directly with soil types.

We could have obtained other results if the variation had been estimated not by the cover of individual species but by ecological groups, but there is as yet no sufficiently clear basis for their objective formation.

The effect of soil and transect differences on vegetative variation had to be determined separately. In a two-factor dispersion analysis it is impossible to unify all this, since, naturally, not every soil type is found in all types of tundra. This fact greatly limits the use of two- and multifactor dispersion analysis in the investigation of ecological systems.

We also decided to ascertain how equivalent the isolated soil units are within the extent of their ecological amplitudes. For this, the dispersions of vegetative variation were determined within the limits of each soil type and compared. Such an operation was done for the same nine types shown in Table 3. In calculation of the dispersions for the soil types, we did not take into account the differences in vegetation on different transects, believing them to be determined by other factors.

A comparison of the dispersions of the nine soil types by means of criterion F showed that only one of 36 dispersion ratios exceeds the 95% credibility level. This is entirely admissible, since in 5% of the cases the selection differences also must exceed the limits of significance. But, on the whole, the matrix of dispersions of vegetation within the soil types can be considered homogeneous. Consequently, the vegetation within the limits of each of the soil types is the same, and they may be considered units of one taxonomic rank.

The method used may be successfully employed also in an analysis of the dependencies of other components of biocenoses. But in connection with the specific distribution of these components by sites and also in connection with a different methodology of calculation, a certain rearrangement of the methodology in selection of field data is called for.

This method permits quantitative measurement of the degree of interdependence of biogeocenotic components. By such means we obtain more definite and clear results than with the use of analysis of the principal components. Its use for estimation of the connection of vegetation with environmental factors has not so far given a sufficiently clear development of the determining factors (Fresco, 1969; van der Maarel, 1969). Moreover, the proposed method is much more simple and practicable. All calculations in one trench may be carried out in one day by one person with the assistance of an abacus and a logarithmic ruler.

CONCLUSIONS

1. In the investigated types of tundra and swamp of the western Taimir, the differences between soil types within the limits of their complexes determine 15-60% of the variation in vegetation. The role of soil differences in determination of the vegetative composition is extremely substantial.

2. Not all isolated soil types bear vegetation differing substantially from that on other soil types.

3. Extremely great differences in vegetation on the same soil type in different types of tundra or in different portions of the same tundral type are determined by other environmental factors: phytocenotic defect and ecological replaceability of species. These features determine 10-50% of the vegetative variation.

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